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Title: Effect of climatic and soil moisture conditions on mushroom productivity and related ecosystem services in Mediterranean pine stands facing climate change

Article Type: Research Paper

Section/Category: Plant physiology, Crop Modelling, water relations including evapotranspiration, WUE, interception

Keywords: fungi; Pinus; global warming; soil water balance; weather; non-wood forest products

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Abstract: Wild mushrooms contribute to a variety of ecosystem services. The expected warmer and drier conditions for the Mediterranean region as a consequence of climate change, are raising concerns about future mushroom productivity due to potential reduction of soil water availability for fungi. The aim of this study was to increase our understanding of the interaction between climate and soil moisture in relation to their impact on mushroom productivity in Mediterranean forests. Mushroom yield data were obtained from 28 permanent mushroom inventory plots intensively monitored in Maritime pine (Pinus pinaster Ait.) stands of northeastern Iberian Peninsula. Annual productivity of total, edible and marketed mushrooms was obtained from measurements conducted every week during the autumn fruiting season for years 2008-2015. Historical weather conditions were obtained through data interpolation from meteorological stations. Soil moisture data were obtained from continuous plot-level measurements. A process-based soil water balance model was used to predict soil moisture under two climate change scenarios, using the predictions of two different regional climate models. Mixed-effects models using either precipitation or soil moisture as predictors, in combination with other weather variables, were fitted to annual mushroom occurrence and yield data. Mushroom yield was primarily dependent on weather and soil moisture conditions during the same month, with the exception of precipitation, whose effects exhibited a one-month delay. High temperatures limited mushroom yield at the beginning of the fruiting season, but tended to enhance it towards the end. The analysis revealed no apparent negative effect of climate change on long-term mushroom productivity, but rather the opposite (i.e., predicted median productivity of marketed mushrooms for 2016-2100 was 23 to 93% higher compared to the current yield), mainly due to an elongation of the fruiting season arising from the combined effect of increased

precipitation at the beginning of the season and warmer temperatures at the end.

Dear Editor,

We are submitting the revised manuscript with reference number AGRFORMET-D-17-00142 entitled "Effect of climatic and soil moisture conditions on mushroom productivity and related ecosystem services in Mediterranean pine stands facing climate change" to be considered for publication in Agricultural and Forest Meteorology journal. The manuscript represents original work not being considered for publication in any other journal.

We have addressed all comments and suggestions raised by the referees which, in our opinion, has contributed to improving the quality and presentation of the paper as well as to further clarifying some aspects that were unclear to the referees. Thus, we have shortened and streamlined the manuscript, moved figures/tables to Appendices, and improved the figures according to the suggestions received. Please, find enclosed with this submission our "Response to Reviewers" letter including our detailed answers to each of the comments provided by the reviewers upon the first peer-review round.

The author to whom correspondence should be addressed is:

Sergio de Miguel

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Sincerely,

Sergio de Miguel (on behalf of all co-authors)

-------------------------------------------------------

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Title page

**Title:**

# Effect of climatic and soil moisture conditions on mushroom productivity and related ecosystem services in Mediterranean pine stands facing climate change

**Authors:**

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**EDITOR'S COMMENTS**

COMMENT
The manuscript is a bit too lengthy. With some editing, the length of the manuscript can be substantially reduced.

ANSWER
The manuscript has been substantially shortened and streamlined by deleting, synthesizing and/or modifying different sections of the manuscript, and by moving information to Supplementary materials.

COMMENT
The article includes too many tables. Perhaps some of the tables can be included in a supplement.

ANSWER
Some tables have been moved to Supplementary materials.

COMMENT
The abstract is a bit too lengthy. In the abstract, the meaning of sentences such as 'Although precipitation-based models showed better fitting statistics than soil moisture-based models, the latter allowed further insight into the drivers of mushroom fruiting' is not clear (this sentence can be eliminated). There are no quantitative results in the abstract.

ANSWER
The abstract has been reduced substantially in order to accommodate it to the recommendations of Agricultural and Forest Meteorology journal and, at the same time, we have further included some relevant quantitative results in the abstract.

COMMENT
All figures need revisions to improve their readability and to make them all consistent. For example, Figure 1a has the y-axis title of 'Mean Squared Deviation' and Figure 1b has the y-axis title of 'Soil moisture in field Capacity'. Only the first letter needs the upper case. Should Figure 1a y-axis have units? The 'a' and 'b' should be put inside the figure boxes. For Figure 2, should there be units for the y-axis? Figures 3 and 4 are not easy to read and are inconsistent compare to the other figures. For example, the y-axis labels are at a different angle compared to the other figures. The yields have no unit. The model name (e.g., CCLM 4.5) should be put inside the box of each figure.

ANSWER
Thank you for your suggestions. All figures have been redone and improved, including those that have been moved to Appendices. We checked axis labels, adding units when possible and using uppercase only in the first letter. We did not move model/rcp names into the box of each figure because to do so the font should be much smaller and, in this particular case, readability would be negatively affected.

COMMENT
There are no units for the quantities provided in Table 5.

ANSWER
Units have been added to that table (i.e., Table 2 in the revised manuscript).

COMMENT
From line 548 to 555, the text needs to be deleted.

ANSWER
The text has been deleted.

COMMENT
The article does not include a summary or conclusions. Is this an oversight?

ANSWER
It is not an oversight. As also acknowledged by the guidelines for authors of Agricultural and Forest Meteorology journal, in scientific publications it is quite common to find that conclusions are embedded for instance within the Discussion section: “The main conclusions of the study may be presented in a short Conclusions section, which may stand alone or form a subsection of a Discussion or Results and Discussion section.”. In this research study, we considered that the best way to address the conclusive remarks was under the form of a subsection embedded within each of the sections in which the Discussion is structured.

**REVIEWER'S COMMENTS**

COMMENT
Reviewer #1: This work reveal interesting long term effects of climate changes on mushroom productivity. As highlithed elsewhere, social benefits from mushroom harvest represent a very important ecosystem service and therefore this research stimulates the debate on whether climate change may or may not represent limiting factors to mushroom productivity. The authors use models to predict long-term changes in those factors affecting mushroom productivity. In particular, a model to predict dynamics of soil water content proved to work well when compared with measured data. References have bene provided, although more details on the model functioning would have been appreciated. The manuscript reads well, with a good English language, and the statistical approaches seem appropriate although I am not an expert in statistical analysis. A couple of comments in detail:

ANSWER
We have much appreciated the acknowledgment made by the reviewer concerning the interest of our research topic in general, and of this study in particular. Although, as suggested by the reviewer, we could of course provide further details on the functioning of the water balance model, the following reasons may advice against expanding the manuscript accordingly: (i) the water balance model used in this study has been already published and explained in much detail in the same journal (see De Cáceres et al., 2015. Coupling a water balance model with forest inventory data to predict drought stress: the role of forest structural changes vs. climate changes. Agric. For. Meteorol. 213, 77–90) and, therefore, readers interested in the specific functioning of this model can easily obtain the required information by accessing that paper; and (ii) the Editor has explicitly asked us to shorten the paper substantially, and providing detailed enough explanations on the water balance model would result in a significant increase of the length of a manuscript that, we agree, it was already a bit too lengthy. Therefore, to avoid contradicting the editor's suggestions, and given that the requested information is already available for readers, we have decided to keep the description of the water balance model brief in the current manuscript. That said, if the Editor considers that the manuscript can be further expanded to accommodate a detailed explanation of the water balance model, we are of course ready to proceed accordingly.

COMMENT
Lines 87-89: not sure the weak point of soil models lies in the evapotranspiration demands only, there are several factors which are critical for proper estimation of water content in soils and good models must be able to predict water circulation based on precipitation inputs, and phisico-chemical properties of soils.

ANSWER
Of course, we fully agree with the reviewer that proper water balance models (i.e., referred to as "soil models" in his/her comment) must be able to predict water circulation based on precipitation inputs and soils properties. This is for instance why, as explained in the manuscript, the water balance model that we used in our study considers both weather and soil conditions in addition to vegetation characteristics when estimating soil moisture. However, this was not the point of our statement in that section of the manuscript. In lines 87-89 of the original manuscript (Introduction section) we just stated that "mushroom yield models considering weather variables only, may fail to capture the actual water availability in the soil as they ignore soil water fluxes, especially those driven by evapotranspiration demands" by citing a relevant paper directly related to the topic and where that idea is

suggested (i.e., Ágreda et al., 2015, Increased evapotranspiration demand in a Mediterranean climate might cause a decline in fungal yields under global warming. Glob. Chang. Biol. 21, 3499–3510.). We think that our statement is correct (and properly referenced) since most mushroom yield modeling efforts based on long-term field monitoring conducted so far in previous research have relied on weather variables only, and not, for instance, on water balance and soil moisture, the latter representing one of the main contributions of our study. In our statement we just try to highlight the need for considering soil moisture (and not precipitation only) when studying fungal dynamics (mushroom productivity included). And, furthermore, we think that our statement does not contradict at all the fact that "good models must be able to predict water circulation based on precipitation inputs, and phisico-chemical properties of soils", with which we fully agree.

COMMENT

Lines 458-460: The occurrence of extreme events is a major threat to mushroom productivity. Considering the long term sampling strategy and the occurrence of extreme events, did you find some experimental evidences of limitation of extreme events? Could models incorporate the stochastic occurrence of extreme events? This is particularly useful since your predictions still foresee a beneficial effect of climate changes on mushroom productivity.

ANSWER

We agree with the reviewer that some extreme weather events may represent a considerable threat to mushroom productivity. However, we think that generalization should be avoided. "Extreme events" as such is a very broad definition that can encompass a wide diversity of "extreme" weather conditions, some of which may have indeed a negative impact on mushroom productivity (e.g., prolonged drought events), but some other may be beneficial for enhancing mushroom productivity (e.g., mushroom experts suggest that intense hail storms can boost mushroom occurrence). That said, the climatic models and climate change projections used in this study indeed considered the stochasticity in the variation of the main weather conditions (e.g., precipitation and temperature) along time, including extreme weather events (e.g., intense drought and rainfall), as shown for instance in Figure 3 of the revised manuscript. Furthermore, as described in the manuscript (e.g., lines 411-413 of the revised manuscript), mushroom yield models also incorporated combinations of predictors accounting for the occurrence of extreme events. Thus, in addition to considering for instance the negative impact of extreme drought conditions by including extremely low monthly precipitation and high temperatures along the mushroom fruiting season in our data and models (see in Table 1 the extreme ranges in the weather data utilized, e.g., September and October precipitation ranging from 0 to 112 mm and from 7 to 235 mm, respectively), we also considered the negative influence of torrential rain events by accounting for the number of rain events associated with a given monthly precipitation, so that the same amount of rainfall results in higher yield if distributed throughout the month (see also in Table 1 the wide ranges for these variables, e.g., number of rainy days in September ranging from 1 to 14). Yet, as also described by the models in the manuscript, torrential precipitation, even if concentrated in a few rain events, will be still more beneficial to mushroom productivity than, for instance, severe drought conditions. In summary, we agree with the reviewer that extreme weather events and their stochasticity need to be considered when estimating and projecting mushroom productivity into future climate change scenarios, and we indeed did our best to consider such events in several and complementary ways based on the available data and information.

**Highlights**

- We study the impact of weather and soil moisture conditions on mushroom yield
- We further explore future trends of mushroom productivity under climate change
- We use a hybrid modeling approach combining process-based and empirical models
- Precipitation was the most significant predictor of annual mushroom productivity
- Models predict higher fungal productivity for 2016-2100 compared to current yield

**Title:**

# Effect of climatic and soil moisture conditions on mushroom productivity and related ecosystem services in Mediterranean pine stands facing climate change

**Authors:**

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## Abstract

Wild mushrooms contribute to a variety of ecosystem services. The expected warmer and drier conditions for the Mediterranean region as a consequence of climate change, are raising concerns about future mushroom productivity due to potential reduction of soil water availability for fungi. The aim of this study was to increase our understanding of the interaction between climate and soil moisture in relation to their impact on mushroom productivity in Mediterranean forests. Mushroom yield data were obtained from 28 permanent mushroom inventory plots intensively monitored in Maritime pine (*Pinus pinaster* Ait.) stands of northeastern Iberian Peninsula. Annual productivity of total, edible and marketed mushrooms was obtained from measurements conducted every week during the autumn fruiting season for years 2008-2015. Historical weather conditions were obtained through data interpolation from meteorological stations. Soil moisture data were obtained from continuous plot-level measurements. A process-based soil water balance model was used to predict soil moisture under two climate change scenarios, using the predictions of two different regional climate models. Mixed-effects models using either precipitation or soil moisture as predictors, in combination with other weather variables, were fitted to annual mushroom occurrence and yield data. Mushroom yield was primarily dependent on weather and soil moisture conditions during the same month, with the exception of precipitation, whose effects exhibited a one-month delay. High temperatures limited mushroom yield at the beginning of the fruiting season, but tended to enhance it towards the end. The analysis revealed no apparent negative effect of climate change on long-term mushroom productivity, but rather the opposite (i.e., predicted median productivity of marketed mushrooms for 2016-2100 was 23 to 93% higher compared to the current yield), mainly due to an elongation of the fruiting season arising from the combined effect of increased precipitation at the beginning of the season and warmer temperatures at the end.

## Keywords

fungi, *Pinus*, global warming, soil water balance, weather, non-wood forest products

## 1. Introduction

Wild mushrooms contribute to a variety of provisioning, cultural and supporting ecosystem services in the Mediterranean Basin and worldwide. On one hand, wild edible mushrooms represent an important food source and may be regarded as a key non-wood forest product (NWFP), especially in the Mediterranean basin where NWFPs are of particular socioeconomic importance (Boa, 2004; Croitoru, 2007). Indeed, in Mediterranean forests, the economic value of mushroom-based ecosystem services, can be much higher than the economic profit traditionally obtained from timber-oriented forestry (Palahí et al., 2009; Martínez de Aragón et al. 2011). Forest fungi also play a critical role in forest ecosystem functioning through their contribution to nutrient and carbon cycles (Mohan et al., 2014; Stokland et al., 2012).

Mushroom yield varies dramatically between years due to variation in the environmental factors that determine the duration of the fruiting season and the frequency of mushroom emergence (Alday et al., 2017; Boddy et al., 2014). Climate arises as the foremost important factor, with precipitation and temperature (and their interaction) having a major impact on mushroom phenology, yield and diversity (Bonet et al., 2012; Büntgen et al., 2015; Kauserud et al., 2008, 2012; Ogaya and Peñuelas, 2005; Taye et al., 2016). However, the effect of climate on mushroom productivity is further modulated by the combined effect of site and soil characteristics and forest stand structure (Martínez-Peña et al., 2012; de-Miguel et al., 2014). The interaction between these factors determines soil moisture, which may be regarded as an integrative driver of mushroom fruiting accounting for different processes resulting in a given mushroom productivity level.

Since fungal fruiting is mainly enhanced by humid and warm conditions, recent trends of temperature increase driven by climate change have been found to enhance yield and earlier mushroom emergence in humid temperate regions, while decreasing and delayed productivity has been observed under drier Mediterranean conditions (Boddy et al., 2014). Future hotter and drier conditions predicted by climate change models for the Mediterranean region (Allen et al., 2014), and the subsequent expected reduction in soil water availability, are likely to enhance drought stress and aridity in forest ecosystems, eventually affecting negatively mushroom productivity (Ágreda et al., 2015; Büntgen et al., 2015). Yet, given the uncertainty about precipitation patterns in climate change scenarios, the reverse could occur if early-autumn drought was not enhanced and the duration of the fruiting season was expanded due to increasing temperature in late autumn.

Climate-sensitive mushroom yield models are in short supply largely due to the lack of long-term monitoring of mushroom yield, especially in drought-prone environments such as the Mediterranean forests (Mohan et al., 2014), although some examples can be found in the literature (e.g., Bonet et al., 2012; Martínez-Peña et al., 2012; Hernández-Rodríguez et al., 2015). Moreover, mushroom yield models considering weather variables only, may fail to capture the actual water availability in the soil as they ignore soil water fluxes, especially those driven by evapotranspiration demands (Ágreda et al., 2015). Nevertheless, long series of soil moisture records in mushroom monitoring plots within forest ecosystems are scarce, since most studies on mushroom productivity are usually lacking such intensive measurements (Boddy et al., 2014). This may constitute a major drawback to our understanding of productivity patterns since modelers are then forced to use precipitation as a surrogate for a more proximal driver. Therefore, in view of the ecological and socioeconomic importance of mushrooms in the Mediterranean basin, a better understanding of the drivers of mushroom productivity is required in order to forecast the provision of the ecosystem services provided by mushrooms, especially within the context of climate change.

In this study, we aim at shading light on the climatic and soil moisture conditions driving mushroom productivity under typical Mediterranean conditions. Moreover, we intend to better understand the role of precipitation *vs* soil moisture in the development of predictive mushroom yield models, in particular: (a) which of the two factors results in models with higher predictive ability; and (b) how mushroom productivity predictions of models using either precipitation or soil moisture differ when projected towards future climates. We address these questions using data from a network of permanent mushroom inventory plots intensively monitored in northeastern Iberian Peninsula, and combining a process-based soil water balance model with mushroom yield statistical models. Analyses were done for three mushroom categories accounting for several ecosystem services; total mushrooms to deduce on the overall productivity (i.e., regulating/supporting services), and edible and marketed mushrooms to deduce on food supply and socioeconomic activity (i.e., provisioning and cultural ecosystem services). All models were projected to future climate conditions using downscaled, bias-corrected climate model predictions.

## 2. Materials and methods

### 2.1 Study area and mushroom inventory plots

The study area is located in the Natural Park of Poblet in Catalonia, North-East Spain (41° 21’ 6.4728 latitude and 1° 2’ 25.7496 longitude). The area is characterized by a coastal Mediterranean climate, with mean annual temperature of 11.8°C, annual rainfall of 665 mm and a pronounced summer drought usually extending from mid-June to mid-September. A set of 28 permanent plots was established between 2008 and 2009 in 50-year-old, even-aged Maritime pine (*Pinus pinaster* Ait.) stands, representing a range of different conditions in stand structure, i.e., stand density from 446 to 2657 trees $ha^{-1}$ and basal area from 20.9 to 81.7 $m^2$ $ha^{-1}$, as well as in elevation (594-1013 m.a.s.l), slope (2-13%) and aspect. Mushroom inventory plots were 100 $m^2$ (10 m × 10 m) in size. Soil is siliceous and has franc-sandy texture. All trees were measured for diameter at 1.3 m breast height (DBH) in December 2010 and re-measured in August 2013.

### 2.2 Mushroom productivity sampling

In each plot, all mushrooms were collected every week between 2008 and 2015 (15 plots) and between 2009 and 2015 (13 plots) during the autumn fruiting season, i.e., from the beginning of September to the end of December, with the majority of the yield being concentrated in October and November. Mushrooms were species-identified, counted and weighted. Total annual yield was classified according to mushroom edibility and marketability categories. Edible mushrooms represented 87% of total mushroom yield, and marketed mushrooms represented, respectively, 43% and 50% of total and edible mushroom production. Marketed mushrooms consisted of seven species, 80% percent of the fresh biomass being represented by *Lactarius* group *deliciosus*. and 13% by *Macrolepiota procera*.

### 2.3 Meteorological data and climate change scenarios

Plot-specific daily weather variables were interpolated from Spanish meteorological stations (1990-2011), and from both Catalan and Spanish stations (1990-2015) following the DAYMET methodology (Thornton and Running, 1999; Thornton et al., 2000), as implemented in the R package ‘meteoland’ (De Cáceres et al., 2017). Daily precipitation, temperature (min, max and average) and relative humidity (min, max and average) were estimated for each plot by averaging the values of several meteorological stations with weighting factors that depended on the geographic proximity to the target plot. The estimate from each meteorological station was further corrected for differences in elevation between the station and the target plot. The high dependence of precipitation on local topography and the distance from weather stations might result in false-predictions of rain events that have not reached the plot, or miss-predictions of rain events which occurred locally at the plot but did not reach the weather stations. This may have an influence on both the estimated probability of occurrence for rain and the intensity of rain events.

Climatic projection data for the period 2016-2100 were obtained from the EU-CORDEX project, available at Earth System Grid Federation (ESGF; http://esgf.llnl.gov/). Daily precipitation, min/max temperature, relative humidity, radiation and wind speed data were assembled according to predictions of the CNRM-CERFACS-CNRM-CM5 global model under representative concentration pathways (RCPs) 4.5 and 8.5, later regionalized to Europe (at 11-km resolution) using CCLM4-8-17 and RCA4 regional dynamic models. As a result, we obtained four alternative climate change scenarios based on the combinations between the two RCPs and the two regional climate models. These predictions were downscaled by correcting for local topography using the 1990-2015 period as reference. Future projected values were corrected for biases calculated monthly for the reference period. In the case of precipitation, correction involved quantile mapping (Gudmunsson et al., 2012). All corrections were conducted using the package 'meteoland' (De Cáceres et al., 2017).

### 2.4 Soil moisture sampling and prediction

Volumetric soil content below-ground was measured using Decagon 5 TM probes (Decagon devices Inc., USA) in each plot. Soil sensors were placed in the middle of each plot, 12-15 cm below-ground, and measurements were recorded every minute and stored as 2-hour average on a data logger EM50 (Decagon devices Inc., USA). Volumetric soil moisture was converted to percentage of moisture relative to field capacity using soil texture and Saxton's pedotransfer equations (Saxton et al., 1986).

Since soil moisture measurements had started in April 2013 and they overlapped only partially with the mushroom collection period, a process-based soil water balance model, available in the R package called 'medfate' (De Cáceres et al., 2015), was used to reconstruct the historical daily series of soil moisture and complete the soil moisture observations for the whole 2008-2015 period. The model requires forest stand characteristics, site and soil variables and meteorological series as inputs. Each individual tree was treated separately, and its height and leaf area index were estimated from DBH according to existing allometric equations for *P. pinaster* (Villanueva, 2004). Soil depth was described in the model using two layers: topsoil (0 – 30 cm) and subsoil (30 – 150 cm). Soil texture was available from plot sampling. Macro-porosity was estimated from sand content and bulk density (Stolf et al., 2011), and values of the latter variables were obtained from the Harmonized World Soil Database (Fao/Iiasa/Isric/Isscas/Jrc, 2009). We used interpolated meteorological series as weather input since this method proved superior to simple assignment of weather data from the closest station, when compared as an input for the soil moisture balance model (results not shown). Since the model does not simulate changes in forest structure, to account for tree growth we simulated soil water balance twice for each stand, using DBH measurements from the two forest inventories. Model predictions for the period prior to the first inventory (i.e., 2008-2010) and after the second inventory (i.e., 2013-2015) were obtained using DBH values from the first and the second inventories, respectively. Predictions for the period between the two inventories were obtained averaging the two simulations, using linear weights based on their relative proximity to each of the inventories.

Topsoil moisture model predictions were validated by comparing them with the field measurements based on the mean squared deviation (MSD) and its partitioning into three additive components; squared bias (SB), non-unity slope (NU) and lack of correlation (LC) (Gauch et al., 2003). The comparison was done using daily and monthly time-steps.

Since model predictions are sensitive to the proportion of fine roots in each soil layer, and this information was lacking, we calibrated these model parameters by determining the distribution of fine roots that maximized the fit to observed soil moisture data in each plot. Specifically, 100 model simulations were done for each plot varying the root proportion in the topsoil between 0.01-0.99 (the proportion of roots in the subsoil was its complement). We selected the distribution of fine roots corresponding to the lowest MSD between observed and predicted soil moisture. Wilcoxon tests indicated a statistically significant reduction in MSD between calibrated and non-calibrated fine root distribution. Finally, a dataset of monthly averages of soil moisture was constructed, incorporating field observations complemented by model predictions for the missing period. Daily meteorological data was also aggregated into monthly values before building mushroom productivity models.

The soil water balance model was also used to obtain soil moisture values corresponding to climate projections (2016-2100). For these simulations, the proportion of fine roots and forest structure (taken from the second inventory) were assumed constant for simplicity.

### 2.5 Mushroom occurrence and productivity modeling

Annual mushroom yield models were developed for the fresh mass of total, edible and marketed mushrooms, using data from the 28 mushroom inventory plots. Monthly values of the following weather variables were used as predictors of annual mushroom yield: cumulative precipitation, number of rainy days, mean temperature, mean maximum and minimum temperature, diurnal temperature difference, mean relative humidity, as well as mean maximum and minimum relative humidity (Table 1). Predictors were selected only if their correlation with mushroom yield was statistically significant, biologically sound and in agreement with current scientific knowledge on forest and fungal ecology, while at the same time avoiding multicollinearity.

We fitted models having either precipitation-related variables or soil moisture variables as factors representing the availability of moisture for fungal fruiting. Thus, we differentiated between precipitation-based and soil moisture-based models by replacing precipitation variables (both cumulative precipitation and number of rainy days) by soil moisture variables. The fitting procedure was based on mixed-effects modeling (Pinheiro and Bates, 2000) using plot random effects to account for between-plot differences. Year random effects were not considered since the productivity of a given plot is mainly driven by annual changes in the monthly weather variables.

The probability of occurrence of mushrooms of any species in a given plot and year was 1 (i.e., for every plot and year, at least some mushrooms emerged during the sampling period). Nevertheless, when focusing on edible or marketed mushroom species, zero annual yield values occurred in several plots and years. This pattern becomes more prominent due to the stochastic nature of mushroom emergence and the rather small size of inventory plots, further increasing the probability for zero yield. Therefore, a two-stage modeling approach was used for modeling annual production of edible and marketed mushrooms, accounting for two separate states (de-Miguel et al., 2014; Hamilton Jr. and Brickell, 1983). The first stage aimed at estimating the probability of mushroom emergence using mixed-effects logistic regression (Eq. 1) with a logit link function (Eq. 2) based on binomially distributed data corresponding to the absence or presence of mushrooms. The second stage aimed at estimating mushroom yield in the log scale, conditional on the former probability of occurrence, using linear mixed-effects modeling (Eq. 3). Snowdon's bias correction factor (Snowdon, 1991) was used when back-transforming model predictions from the log scale to the original productivity units (i.e., kg $ha^{-1}$ $yr^{-1}$).

The final production models result from the multiplication of the probability of mushroom occurrence by the mushroom yield conditional on the probability of occurrence (Eq. 4), thus reflecting a combined effect of two separate states able to reveal potential differences concerning the effect of weather and soil moisture variables within each state.

Eq. (1) $$\mathrm{P}(\mathrm{y} = 1|\mathrm{x})_{ij} = \pi(\mathrm{x}) = \frac{1}{1+ e^{-[(\alpha_0+a_{0i})+\alpha\mathbf{X}_1]}}$$

Eq. (2) $$\mathrm{g}(\mathrm{x}) = \log\left[\frac{\pi(\mathrm{x})}{1-\pi(\mathrm{x})}\right] = (\alpha_0 + a_{0i}) + \alpha\mathbf{X}_1$$

Eq. (3) $$log(yield_c)_{ij} = (\beta_0 + b_{0i}) + \beta\log(\mathbf{X}_2) + \varepsilon$$

Eq. (4) $$yield_{ij} = \pi(\mathrm{x}) \times e^{\log(\mathrm{yield}_c)} \times Snowdon$$

where $\mathrm{P}(\mathrm{y} = 1|\mathrm{x})$ is probability of occurrence of edible or marketed mushrooms in plot *i* and year *j*, $(yield_c)_{ij}$ is yield (kg $ha^{-1}$ $yr^{-1}$) conditional on the probability of occurrence of mushrooms, $yield_{ij}$ is total, edible or marketed mushroom yield (kg $ha^{-1}$ $yr^{-1}$) in plot *i* and year *j*, $\alpha$ and $\beta$ denote fixed-effects model parameters, $a_0$ and $b_0$ denote plot random effects, $\mathbf{X}_1$ and $\mathbf{X}_2$ are vectors of predictor variables, $\varepsilon$ is residual following a normal distribution with mean equal to zero and variance equal to $\sigma^2$, and $Snowdon$ is the correction factor of the back-transformation bias.

Model selection followed an iterative, systematic procedure based on forward selection of predictors upon fitting statistics, considering the significance of model parameters (t-value $\geq 2$, p-value $\leq 0.05$), likelihood-ratio tests and residual standard error, while avoiding multicollinearity. Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) were used for variable selection in order to prevent overfitting and construct parsimonious models. The predictive ability of logistic models was further assessed by computing their receiver operating characteristics (ROC) curve and the corresponding area under the curve (AUC). Yield models were further evaluated by partitioning their MSD in three additive components; SB, NU and LC (Gauch et al., 2003). All data analyses and model fitting were performed in R software 3.2.2 (R Development Core Team, 2015). Mixed-effects models were fitted using "glmer" and "lmer" functions of "lme4" package (Bates et al., 2014).

**Table 1.** Summary of the main data used.

| Model Variables | Mean | SD | Minimum | Maximum |
|---|---|---|---|---|
| Total mushroom yield (kg ha$^{-1}$ yr$^{-1}$) | 86.37 | 102.17 | 0.01 | 481.61 |
| Edible mushroom yield (kg ha$^{-1}$ yr$^{-1}$) | 74.92 | 97.79 | 0.00 | 459.45 |
| Marketed mushroom yield (kg ha$^{-1}$ yr$^{-1}$) | 37.09 | 72.63 | 0.00 | 452.24 |
| Total mushroom occurrence (probability) | 1.00 | 0.00 | 1.00 | 1.00 |
| Edible mushroom occurrence (probability) | 0.94 | 0.24 | 0.00 | 1.00 |
| Marketed mushroom occurrence (probability) | 0.70 | 0.46 | 0.00 | 1.00 |
| August precipitation (mm) | 12.45 | 10.92 | 0.00 | 35.28 |
| September precipitation (mm) | 49.42 | 32.92 | 0.21 | 111.73 |
| October precipitation (mm) | 58.13 | 62.39 | 6.88 | 235.37 |
| November precipitation (mm) | 101.43 | 74.52 | 0.28 | 208.06 |
| September number of rainy days (days) | 7.92 | 4.54 | 1.00 | 14.00 |
| October number of rainy days (days) | 8.00 | 3.36 | 4.00 | 14.00 |
| November number of rainy days (days) | 9.47 | 5.80 | 2.00 | 25.00 |

| | | | | |
|---|---|---|---|---|
| November mean temperature (°C) | 8.53 | 1.86 | 3.98 | 11.96 |
| December mean temperature (°C) | 5.09 | 1.59 | 1.08 | 7.80 |
| September mean maximum temperature (°C) | 22.33 | 2.90 | 15.37 | 27.71 |
| October mean maximum temperature (°C) | 17.77 | 2.22 | 12.23 | 21.83 |
| November mean minimum temperature (°C) | 4.14 | 1.73 | 0.83 | 7.32 |
| December mean minimum temperature (°C) | 0.71 | 1.29 | -2.68 | 3.03 |
| September mean relative humidity (%) | 67.02 | 4.18 | 59.32 | 76.24 |
| September mean maximum relative humidity (%) | 95.72 | 2.28 | 90.23 | 98.85 |
| September mean soil moisture (% of field capacity) | 0.48 | 0.12 | 0.24 | 0.81 |
| October mean soil moisture (% of field capacity) | 0.60 | 0.19 | 0.24 | 0.93 |

Future mushroom productivity was predicted based on the predicted monthly weather and soil moisture variables under the four climate change scenarios. To prevent illogical predictions in extrapolation from the empirical mushroom yield models, predicted weather conditions for the period 2016-2100 were truncated according to the minimum and maximum values observed for the corresponding weather variables during the historical period 2008-2015.

## 3. Results

### 3.1 Water balance model and soil moisture estimation

Soil moisture predictions of the water balance model matched reasonably well the values measured in the plots, with the single exception of plot #22, which exhibited higher MSD (Fig. S1). The high bias for this particular plot was probably caused by its extreme gross texture and high rock content (which might result from an unrepresentative soil texture sample) leading to very low water holding capacity and strong fluctuation of soil moisture values. Therefore, for this specific plot, we opted for discarding the predicted soil moisture values and rely on measured soil moisture only. The proportion of fine roots distributed between topsoil and subsoil was calibrated for each plot, reducing significantlly the MSD values. As a result, the average MSD was 0.025.

### 3.2 Models for total mushroom production

The information about model parameter estimates and predictors of total mushroom yield are presented in Table S1. The precipitation-based model (residual variance 1.031, random effects variance 0.330) performed better than the soil moisture-based model (residual variance 1.690, random effects variance 0.287), and the root mean squared deviation (RMSD) was 83.2 kg $ha^{-1}$ $yr^{-1}$ and 98.7 kg $ha^{-1}$ $yr^{-1}$, respectively. For both models SB was zero, and the most of the error was derived from LC, which was higher in the soil moisture-based model, whereas NU was slightly lower in the latter model (Fig. 1).

In the precipitation-based model, the rainfall of September, together with the accumulated number of rainy days in September, October and November, had a significant positive influence on total mushroom yield. The combined effect of November and December's mean minimum temperature had a significant positive effect on mushroom yield, so that the higher the mean minimum temperatures the higher the yield.

The soil moisture-based model included a wider variety of predictors, compared to the precipitation-based model. Total annual mushroom yield was positively correlated with soil moisture of October, the combined effect of November and December's mean minimum temperature, and the mean maximum relative humidity of September. Furthermore, the model revealed a negative effect of the sum of mean maximum temperatures of September and October, meaning that the lower the maximum temperatures of late summer and early autumn the higher the observed yield.

## 3.3 Models for edible mushroom occurrence and productivity

The information about the models of edible mushroom yield is presented in Table S2, for both probability of occurrence and yield conditional on occurrence models. The probability of occurrence of edible mushrooms in the precipitation-based model (AUC= 0.90) was positively correlated with the number of rainy days in October and the sum of the mean temperature of November and December. The yield conditional on occurrence model (residual variance 1.340, plot random effects variance 0.520) shared similar predictors with the total mushroom yield model. The root mean squared deviation (RMSD) was 85.7 kg $ha^{-1}$ $yr^{-1}$, SB was zero and the majority of error was derived from LC (Fig. 1).

The probability of occurrence of edible mushrooms in the soil moisture-based model (AUC= 1.00) was positively correlated with the soil moisture in October and the mean minimum temperature of November and December. The yield conditional on occurrence model (residual variance 1.941, plot random effects variance 0.468) differed from the total mushroom yield model only in variable transformation. Moreover, it shared similar predictors with the probability of occurrence model with the sole addition of the positive influence of maximum relative humidity of September. The RMSD was 88.0 kg $ha^{-1}$ $yr^{-1}$. SB was zero, the majority of error was derived from LC, and NU was lower compared to the precipitation-based model (Fig. 1).

## 3.4 Models for marketed mushroom occurrence and productivity

The information about the models of marketed mushroom yield is presented in Table S3, for both the probability of occurrence and yield conditional on occurrence. The probability of mushroom occurrence in the precipitation-based model (AUC = 0.96) was positively correlated with the number of rainy days in September, the rainfall in October and the mean minimum temperature of November. The yield conditional on occurrence model (residual variance 1.367, plot random effects variance 0.724) consisted of two main differences compared to the probability of occurrence model; an increasing-decreasing influence of the rainfall in October suggesting that extreme high values of precipitation might cause a decrease in the yield of marketed mushrooms, and a positive influence of November's mean temperature only. The RMSD was 51.3 kg $ha^{-1}$ $yr^{-1}$. SB was zero, NU virtually zero, while the error was almost completely derived from LC (Fig. 1).

The probability of mushroom occurrence, according to the soil moisture-based model (AUC = 0.93), was positively influenced by the combined effect of soil moisture in September and October and the mean minimum temperature of November, while negatively affected by the mean maximum temperature of October. The yield conditional on occurrence model (residual variance 1.861, plot random effects variance 0.768) showed to be positively influenced by soil moisture of October and mean maximum temperature of November, while negatively affected by mean maximum temperature of October. The RMSD was 69.7 (kg $ha^{-1}$ $yr^{-1}$). SB and NU were zero, while the whole error was derived from LC (Fig. 1).

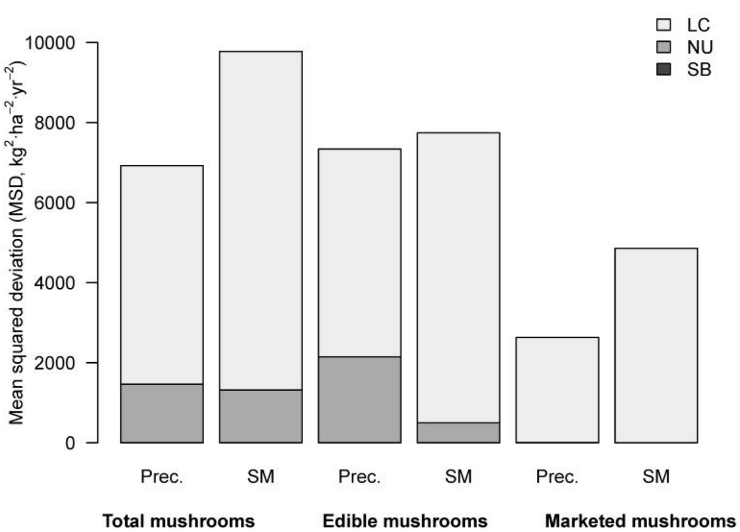

**Figure 1.** Mean squared deviation (MSD) of precipitation-based (Prec.) and soil moisture-based (SM) mushroom yield models, for the three mushroom categories (total, edible and marketed), resulting from the difference between observed mushroom yield and model-based predictions. The MSD is partitioned in three additive components; Squared Bias (SB), Non-unity Slope (NU) and Lack of Correlation (LC) based on Gauch et al. (2003)

**Table 2. Medians of future (2016-2100) mushroom productivity (kg ha$^{-1}$ yr$^{-1}$)** as predicted by the precipitation- and soil moisture-based yield models according to the four climate change scenarios resulting from the two representative concentration pathways (RCPs) 4.5 and 8.5, and the regionalization conducted with the two alternative models CCLM4-8-17 and RCA4.

| | | RCP 4.5 (2016-2100) | | RCP 8.5 (2016-2100) | |
|---|---|---|---|---|---|
| Mushroom group | Yield model | CCLM | RCA4 | CCLM | RCA4 |
| Total | Precipitation-based | 72.00 | 52.67 | 70.12 | 73.59 |
| | Soil moisture-based | 251.55 | 306.57 | 178.84 | 290.93 |
| Edible | Precipitation-based | 57.33 | 43.11 | 59.55 | 59.55 |
| | Soil moisture-based | 174.18 | 239.70 | 137.90 | 223.79 |
| Marketed | Precipitation-based | 45.38 | 43.67 | 42.74 | 60.90 |
| | Soil moisture-based | 67.00 | 66.01 | 63.84 | 74.42 |

### 3.5 Future mushroom productivity under climate change

Unexpectedly, the predicted mushroom productivity for the period 2016-2100 revealed a positive effect of climate change on long-term mushroom productivity. We found increasing mushroom yield for all mushroom categories under the four combinations of climate change scenarios and regional climate models (Fig. 2). A detailed inspection of the effect of climate change scenarios on the main predictors of mushroom yield revealed that, whereas autumn precipitation and soil moisture are expected to remain more or less stable (or even increase slightly) during the fruiting season along the 2016-2100 period, the temperatures are expected to increase, as compared to the historic period 2008-2015 (Fig. 3).

Soil moisture-based models resulted in higher mushroom productivity predictions as compared to the precipitation-based equations, although these differences were much smaller for the group of marketed mushrooms. We also found contrasting results between climate change scenarios and climate regionalization models in relation to the mushroom yield models (Table 2). Thus, we found that future mushroom yield, as represented by the median productivity predicted from precipitation-based models, was always higher in the most drastic RCP in terms of temperature change (RCP 8.5) when the RCA4 climate regionalization model was used, whereas differences between RCPs were minimal when using the CCLM4-8-17 model. Conversely, future mushroom productivity predicted from soil moisture-based models tended to be lower for RCP 8.5 than for RCP 4.5 regardless of the climate regionalization model, except for the case of marketed mushrooms when using the RCA4 model. For RCP 8.5, future mushroom productivity from both precipitation- and soil moisture-based models tended to be always higher for the RCA4 model than for the CCLM4-8-17 model. In contrast, for RCP 4.5, the RCA4 model resulted in lower mushroom productivity when coupled with precipitation-based models, whereas the CCLM4-8-17 model resulted in higher total and edible mushroom yield using soil moisture-based models.

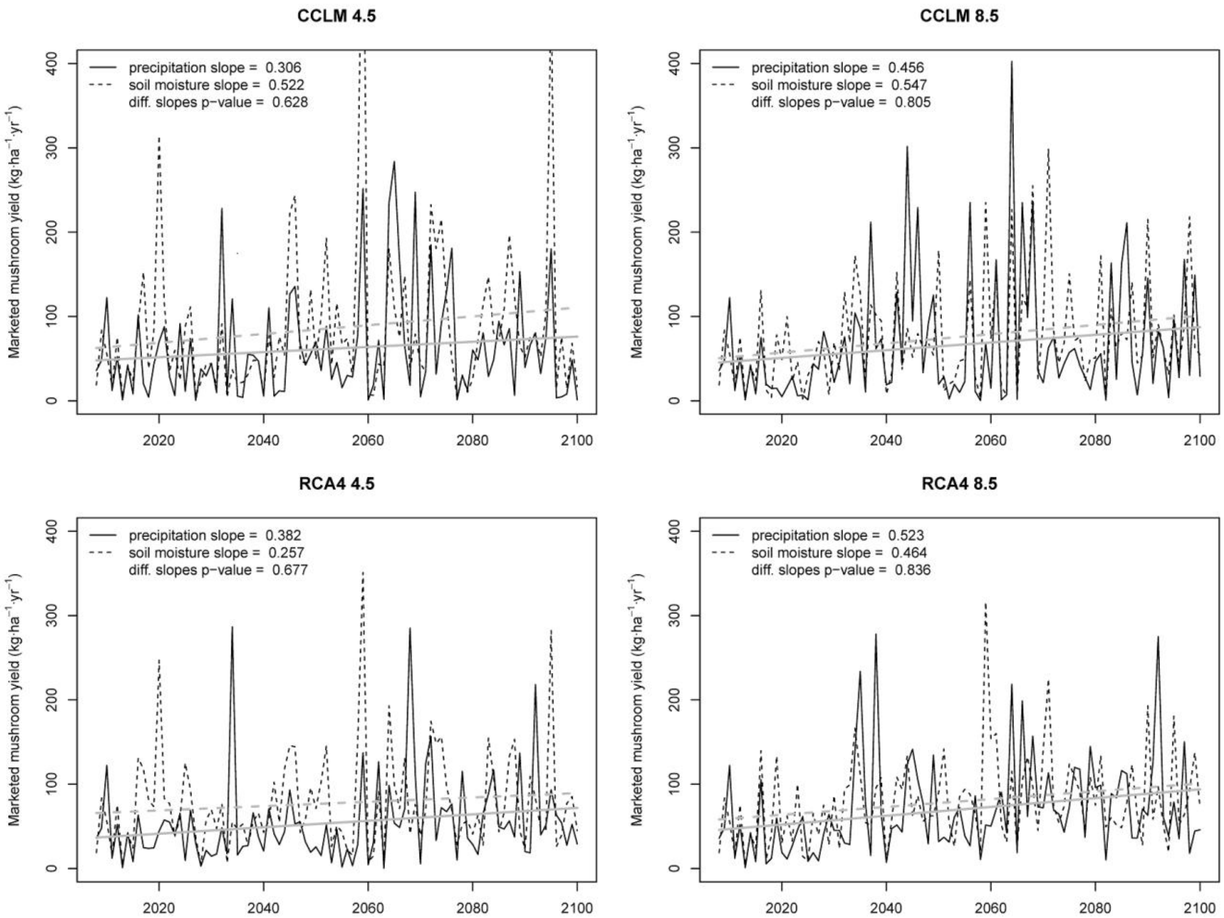


**Figure 2.** Predicted annual productivity of marketed mushrooms under the four climate change scenarios according to the precipitation-based (black solid line) and soil moisture-based (black dashed line) yield models. The grey solid and dashed lines represent the overall trend of marketed mushroom productivity from 2008 to 2100 according for both yield models, respectively.

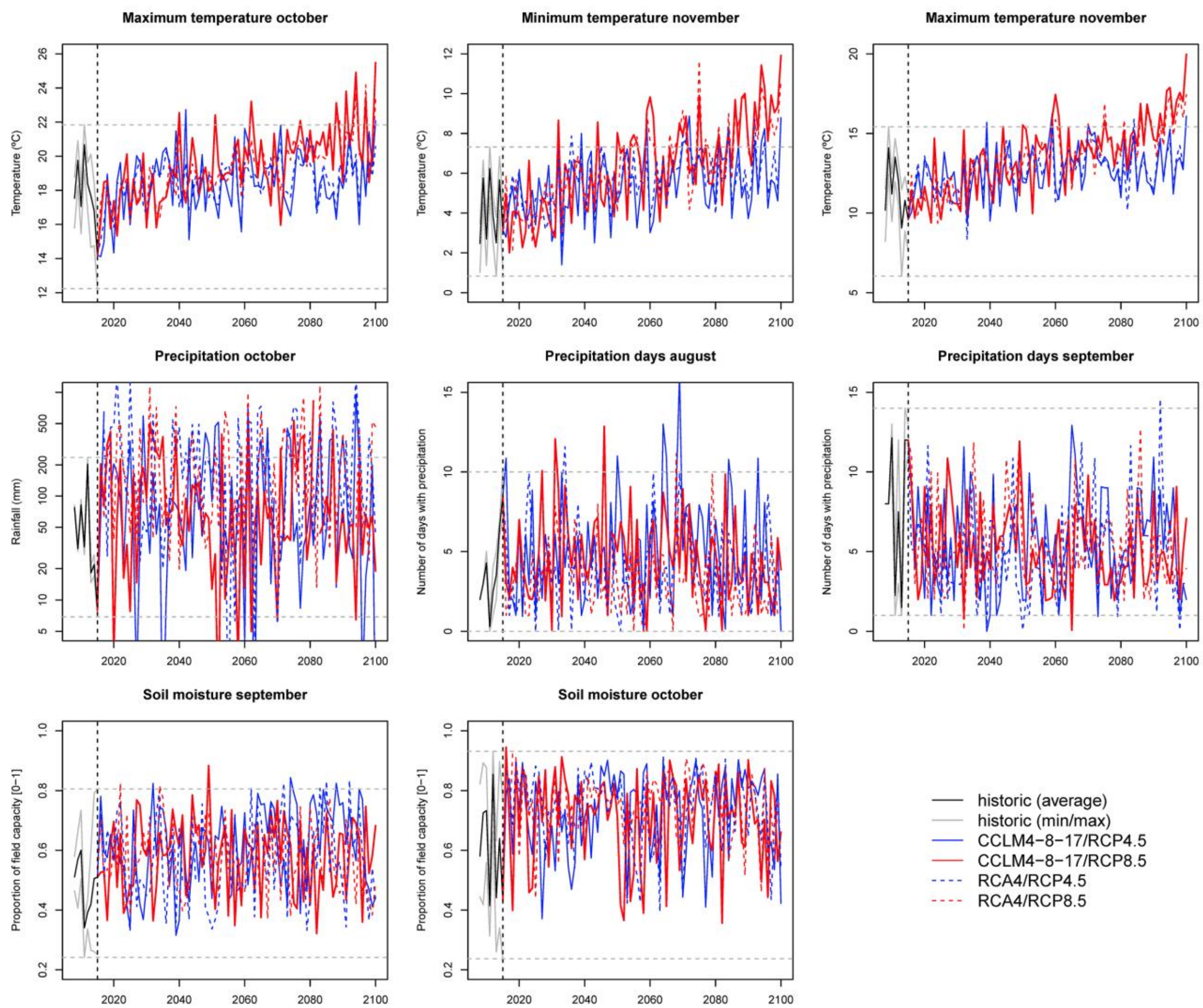


**Figure 3.** Projected climatic and soil moisture predictors of marketed mushrooms for the period 2016-2100 under the two climate change scenarios (RCPs 4.5 and 8.5) and following the predictions of two regional climate models (CCLM4-8-17 and RCA4). Historic values during the mushroom inventory period (2008-2015) are also shown for comparison.

## 4. Discussion

### 4.1 Differences between yield and occurrence models and between mushroom categories

Total and edible mushroom yield were related to the same set of predictors in both precipitation- and soil moisture-based models. This is logical since edible mushrooms represented 87% of total mushroom biomass. In contrast, marketed mushroom yield was related to a different set of predictors. Moreover, 93% of marketed mushrooms consisted of *L.* group *deliciosus* and *M. procera*, which implies that the latter models are mainly driven by the ecological requirements of these fungal species only. The predictors included in marketed mushroom models shifted one month earlier compared with those included in total and edible mushroom models. Namely, the precipitation-based model included August's precipitation and excluded November's, while the soil moisture-based model included the soil moisture of September in addition to October's. Furthermore, both excluded the temperatures in December, being the last month of the fruiting season. These results indicate on an earlier phenology of the marketed species and match the fact that *M. procera* fruit early in the season and is exclusively responsible for the marketed yield of September in our study area.

Models for probability of occurrence and models for yield differed in their predictors. Generally, yield models accommodated a larger number of predictors covering the extent of the whole fruiting season, while only a narrower time frame was required for the occurrence of mushrooms. Thus, regarding marketed mushrooms, the precipitation-based model for the probability of mushroom occurrence showed a dependence on the precipitation in September and October and the temperature in November, while an increase in yield resulted from the addition of precipitation of August, which may positively affect the early fruiting of *M. procera* in September. Another interesting difference was the increasing-decreasing effect of precipitation in October only present in the yield model. This suggests that while precipitation is essential for mushroom occurrence, the effect on the yield can turn negative in excessive wet conditions for some species (Boddy et al., 2014) which may be due to reduced soil aeration (Moore et al., 2008).

### 4.2 Effect of weather and soil moisture variables on mushroom occurrence and productivity

Precipitation and temperature variables were the most important predictors of mushroom emergence and yield. In the Mediterranean, mushroom production is limited in the beginning of the season (September-October) by high temperatures and low rainfall, that is, by a prolongation of summer drought. Thus, the extension of summer-like weather during the fruiting season diminishes the production (Büntgen et al., 2015). Thus, fungal communities in Mediterranean ecosystems may already be experiencing a delayed phenology and reduced production for these reasons as a result of climate change (Boddy et al., 2014). On the other hand, in the end of the season (November-December), when precipitation and water availability in the soil are sufficient for mushroom fruiting, the production is more limited by low temperatures. Hence, cold temperatures in these months may be related to decreasing mushroom yield (Hernández-Rodríguez et al., 2015). While, in the literature, the effect of temperature on mushroom yield is reported as variable (Boddy et al., 2014), we found that there is no contradiction in having both positive and negative effects during a single fruiting season.

Interestingly, in most cases our models indicated that the mean maximum and minimum temperatures for September-October and November-December, respectively, are more significant predictors than mean temperatures. While agreeing with previous research regarding a non-linear effect of temperature on fungal development (Boddy et al., 2014), these findings also suggest a greater sensitivity of mushroom fruiting to daily extreme temperatures over mean temperatures, so that the exposure to extreme weather events might result in a greater inhibition of observed production.

The number of rainy days in a particular month often revealed as a more significant predictor than the cumulative rainfall since it accounts for both the amount of precipitation as well as for its temporal distribution. In all models, precipitation (i.e., cumulative rainfall and number of rainy days) exhibited a one-month time lag in its correlation with mushroom productivity, that is, it became a significant factor affecting one month before the start of the mushroom season, and ceased to be significant one month before the end of the season. This is in agreement with previous research indicating a one month delay in the effect of rain events on mushroom yield in the Mediterranean (Bonet et al., 2012, 2010; Martínez de Aragón et al., 2007; Taye et al., 2016).

In all our models, soil moisture appeared as a significant mushroom predictor one month later than precipitation did, thus matching the initiation of fruitbody production. Soil moisture follows rainfall event's intensity (Ogaya and Peñuelas, 2005), and showed a positive correlation with precipitation of the same and previous month. Nevertheless, maximum relative humidity, and not soil moisture, was significant in the month prior to fruiting (probably due to high correlation with precipitation), indicating that precipitation is probably influencing mushroom yield mainly by increasing soil moisture. The delay between precipitation events and mushroom yield might be explained by the necessity to first acquire enough fruiting potential before the initiation of fruit bodies (Krebs et al., 2008; Salerni et al., 2002).

It is worth highlighting that our data also showed an off-season effect of weather on mushroom productivity, exhibiting a highly negative relationship between precipitation in March (and to lesser extent in the whole spring) and autumn mushroom productivity. However, we could not find any support in the literature for such negative effect. On the other hand, spring precipitation was negatively correlated with autumn precipitation, an accepted fundamental driver of mushroom fruiting in the autumn season. Moreover, carbon from photosynthetic activity arrives to symbiotic fungi within days (Högberg et al., 2008; Leake et al., 2001). For all these reasons, we disregarded the negative effect of March precipitation on autumn mushroom yield as a statistical artifact rather than a true effect, further raising skepticism regarding such an off-season effect on mushroom productivity, reported in previous research (e.g., Primicia et al., 2015). A similar statistical artifact occurred regarding the effect of soil moisture on mushroom yield. During the colder months of the fruiting season (Nov-Dec), high values of soil moisture were associated with low mushroom yield, not because of a true negative effect of soil moisture, but rather due to the effect of low temperatures, which decrease soil drying rates but also inhibit fungal fruiting. This interaction produced an illogical negative correlation between soil moisture and mushroom productivity. In consequence, although soil moisture is known to be a crucial driver of fungal development and fruiting, its effect in our models was limited to rather warm months solely (i.e., Sept-Oct).

### 4.3 Climate change and mushroom productivity

Previous research has raised concerns about the potential negative effect of climate change on future mushroom productivity, with strong implications on the provision of mushroom-based ecosystem services related to the socioeconomic activities surrounding mushroom picking and trade. Indeed, some studies have highlighted that mushroom productivity in Mediterranean ecosystems may be experiencing a sharp drought-induced decrease (Ágreda et al., 2015; Boddy et al., 2014) due to delayed phenology in the autumn season (Büntgen et al., 2015; Kauserud et al., 2012). This could affect more severely the group of marketed mushrooms since, as described above, some of the earliest edible species to fruit belong to this category. However, our results reflect a different trend, namely, that mushroom productivity in the study area may be enhanced under most of the climate change scenarios analyzed. The predicted positive impact of global warming on mushroom productivity arises from the effect of the main variables that drive mushroom occurrence and yield, which results in an elongation of the mushroom fruiting season rather than a shortening associated with a delayed phenology. Thus, in the evaluated scenarios (i.e., ranging from the less severe RCP 4.5 to the most drastic RCP 8.5), the amount of rainfall at the beginning of the season is predicted to remain more or less stable (or even increase slightly) until 2100, despite the inter-annual fluctuations. Although the climatic models also predict a slight reduction of the number of rainy days, therefore resulting in more intense rain events, in most cases this does not seem to be relevant enough to hinder mushroom productivity. Furthermore, the models predict increased temperatures at the end of the fruiting season, when cold weather conditions often inhibit mushroom emergence and growth, which would contribute to expanding the mushroom fruiting season. Interestingly, these effects are more exacerbated in the most drastic RCP 8.5, which in general results in higher expected mushroom productivity for the period 2016-2100. However, there is uncertainty about the actual extent of these effects inasmuch as, in addition to the intrinsic uncertainty associated to any global warming scenario, we found considerable differences (and in a few cases, opposite trends) in future mushroom yield predictions among the two models (CCLM4-8-17 and RCA4) used for the regionalization of the global climate model predictions. Moreover, the response of mushroom fruiting to climate change may be fungal species-specific according to the ecological requirements of each taxon.

### 4.4 Causal drivers *versus* predictive variables of mushroom productivity

It is worth highlighting the relevance of distinguishing between causal drivers and predictors of mushroom productivity. Precipitation is not the most proximal causal driver of fungal development compared to soil moisture, but precipitation variables proved more significant predictors of mushroom productivity. Thus, it seems that rain events integrate several important causal drivers, such as a positive influence on soil moisture and relative humidity, and negative or positive effect on temperature. Soil moisture-based models, which included soil moisture instead of precipitation variables, had lower explanatory power than precipitation-based models (Figure 5). Nevertheless, soil moisture-based models provided a more profound insight into mushroom production dynamics. Since soil moisture did not correlate as strongly with other variables as precipitation did, model selection led to the inclusion of predictors that were not selected in the precipitation-based models, and sharpened the effect of others. For example, soil moisture-based models refined the negative effect of low mean temperatures in November and October, revealing the high sensitivity of edible mushroom emergence to extreme temperatures by replacing the predictor of mean temperature by minimum temperature. Similarly, the negative effect of maximum temperatures in September and October on total mushroom production, and the positive influence of relative humidity in September on total and edible mushroom yield only appeared significant when accounting for soil moisture instead of precipitation in the models. Therefore, our results suggest that the inclusion of precipitation as a predictor, while having great predictive ability, may obscure the effect of several mushroom fruiting drivers because of the correlation between precipitation and these drivers. On the other hand, precipitation-based models may be used when the main aim is yield prediction.

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**SUPPLEMENTARY MATERIAL**

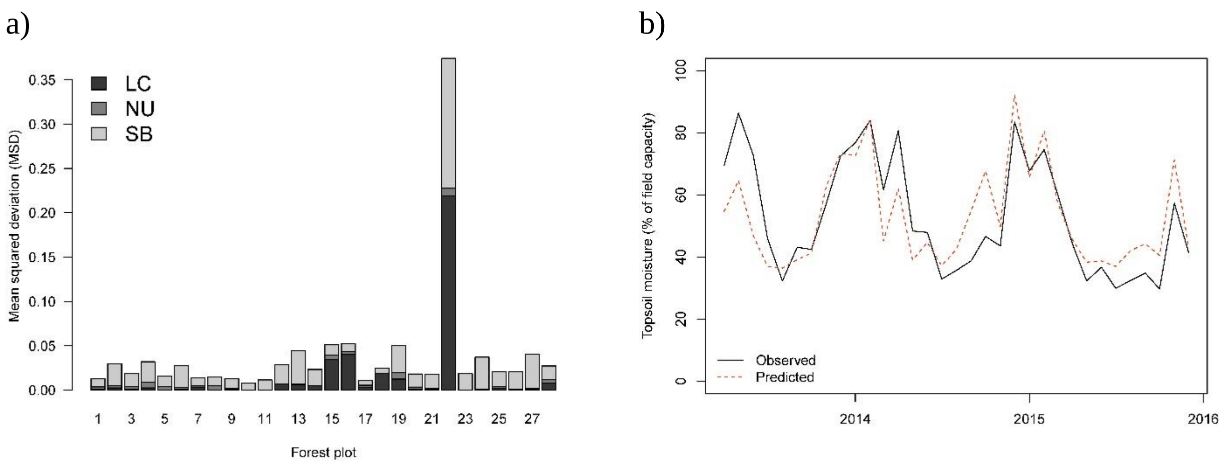


**Figure S1.** a) Mean squared deviation (MSD; in squared proportion of field capacity) of soil moisture predictions for each forest plot, resulting from the difference between measured soil moisture values and the predictions from the process-based water balance model after calibration. MSD values are partitioned in three additive components; Squared Bias (SB), Non-unity Slope (NU) and Lack of Correlation (LC), based on Gauch et al (2003). b) Comparison of predicted and observed monthly mean soil moisture over three years, an example using plot #11.

**Table S1.** Fixed parameter estimates of the precipitation- and soil moisture-based models, describing the relationship between total mushroom yield and climatic and soil moisture predictors. *P* is cumulative precipitation, whereas *raindays* is the number of rainy days in a given month. *Tmin* and *Tmax* are, respectively, the mean minimum and maximum temperature of a given month. *RHmax* is mean maximum relative humidity, and *SM* is mean soil moisture in a given month. Numbers 9 to 12 correspond to the months of the year ranging from September to December, respectively.

| Model | Eq. | Predictor | Coef. | Estimate | St. error | T value |
|---|---|---|---|---|---|---|
| Precipitation-based | 3 | Intercept | $\beta_0$ | -5.498 | 0.615 | -8.945 |
| | | *P* 9 | $\beta 1$ | 0.022 | 0.002 | 9.337 |
| | | log(*raindays* 9+ *raindays* 10+ *raindays* 11) | $\beta 2$ | 2.096 | 0.205 | 10.195 |
| | | (*Tmin* 11+*Tmin* 12) | $\beta 3$ | 0.259 | 0.029 | 8.791 |
| Soil moisture-based | 3 | Intercept | $\beta_0$ | -29.849 | 4.835 | -6.173 |
| | | *SM* 10 | $\beta 1$ | 2.536 | 0.600 | 4.224 |
| | | (*Tmax* 9+*Tmax* 10) | $\beta 2$ | -0.225 | 0.029 | -7.710 |
| | | (*Tmin* 11+*Tmin* 12) | $\beta 3$ | 0.445 | 0.046 | 9.634 |
| | | *RHmax* 9 | $\beta 4$ | 0.403 | 0.058 | 6.939 |

**Table S2.** Fixed parameter estimates of the precipitation- and soil moisture-based models describing the relationship between edible mushroom yield and climatic and soil moisture variables. *P* is cumulative precipitation, whereas *raindays* is number of rainy days in a given month. *T*, *Tmin* and *Tmax* are, respectively, mean, mean minimum and mean maximum temperature of a given month. *RHmax* is mean maximum relative humidity, and *SM* is mean soil moisture in a given month. Numbers 9 to 12 correspond to the months of the year ranging from September to December, respectively.

| Model | Eq. | Predictor | Coef. | Estimate | St. error | T value | P value |
|---|---|---|---|---|---|---|---|
| Precipitation-based | 1 | Intercept | $\alpha_0$ | -13.135 | 4.188 | | 0.002 |
| | | sqrt(*raindays* 10) | $\alpha 1$ | 3.388 | 1.301 | | 0.009 |
| | | sqrt(*T* 11+*T* 12) | $\alpha 2$ | 2.291 | 0.718 | | 0.001 |
| Precipitation-based | 3 | Intercept | $\beta_0$ | -5.828 | 0.842 | -6.921 | |
| | | *P* 9 | $\beta 1$ | 0.025 | 0.002 | 9.237 | |
| | | log(*raindays* 9+ *raindays* 10+ *raindays* 11) | $\beta 2$ | 2.031 | 0.260 | 7.794 | |
| | | (*Tmin* 11+*Tmin* 12) | $\beta 3$ | 0.269 | 0.037 | 7.251 | |
| Soil moisture-based | 1 | Intercept | $\alpha_0$ | -17.008 | 12.630 | | 0.178 |
| | | sqrt(*SM* 10) | $\alpha 1$ | 44.221 | 21.509 | | 0.040 |
| | | (*Tmin* 11+*Tmin* 12) | $\alpha 2$ | 9.722 | 2.628 | | 0.000 |
| Soil moisture-based | 3 | Intercept | $\beta_0$ | -184.915 | 28.923 | -6.393 | |
| | | sqrt(*SM* 10) | $\beta 1$ | 3.243 | 1.023 | 3.168 | |
| | | (*Tmax* 9+*Tmax* 10) | $\beta 2$ | -0.235 | 0.034 | -6.869 | |
| | | (*Tmin* 11+*Tmin* 12) | $\beta 3$ | 0.425 | 0.057 | 7.352 | |
| | | log(*RHmax* 9) | $\beta 4$ | 42.313 | 6.593 | 6.417 | |

**Table S3.** Fixed parameter estimates of the precipitation- and soil moisture-based models describing the relationship between marketed mushroom yield and climatic and soil moisture variables. *P* is cumulative precipitation, whereas *raindays* is the number of rainy days in a given month. *T*, *Tmin* and *Tmax* are, respectively, the mean, mean minimum and mean maximum temperature of a given month. *SM* is mean soil moisture in a given month. Numbers 8 to 11 correspond to the months of the year ranging from August to November, respectively.

| Model | Eq. | Predictor | Coef. | Estimate | St. error | T value | P value |
|---|---|---|---|---|---|---|---|
| Precipitation-based | 1 | Intercept | $\alpha_0$ | -7.589 | 1.591 | | 0.000 |
| | | *raindays* 9 | $\alpha 1$ | 0.466 | 0.079 | | 0.000 |
| | | log(*P* 10) | $\alpha 2$ | 1.144 | 0.286 | | 0.000 |
| | | *Tmin* 11 | $\alpha 3$ | 0.369 | 0.148 | | 0.013 |
| Precipitation-based | 3 | Intercept | $\beta_0$ | -9.236 | 1.634 | -5.652 | |
| | | (*raindays* 8+ *raindays* 9) | $\beta 1$ | 0.127 | 0.021 | 5.949 | |
| | | *P* 10 | $\beta 2$ | -0.045 | 0.007 | -6.086 | |
| | | sqrt(*P* 10) | $\beta 3$ | 1.006 | 0.137 | 7.311 | |
| | | log(*T* 11) | $\beta 4$ | 2.823 | 0.626 | 4.508 | |
| Soil moisture-based | 1 | Intercept | $\alpha_0$ | 1.909 | 2.258 | | 0.398 |
| | | (*SM* 9+*SM* 10) | $\alpha 1$ | 6.847 | 1.217 | | 0.000 |
| | | *Tmax* 10 | $\alpha 2$ | -0.624 | 0.151 | | 0.000 |
| | | *Tmin* 11 | $\alpha 3$ | 0.784 | 0.204 | | 0.000 |
| Soil moisture-based | 3 | Intercept | $\beta_0$ | -3.099 | 2.491 | -1.244 | |
| | | log(*SM* 10) | $\beta 1$ | 1.859 | 0.446 | 4.169 | |
| | | *Tmax* 10 | $\beta 2$ | -0.285 | 0.127 | -2.245 | |
| | | *Tmax* 11 | $\beta 3$ | 4.839 | 1.661 | 2.913 | |